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RNA-seq highlights parallel and contrasting patterns in the evolution of the nuclear genome of fully mycoheterotrophic plants

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Abstract

Background: While photosynthesis is the most notable trait of plants, several lineages of plants (so-called full heterotrophs) have adapted to obtain organic compounds from other sources. The switch to heterotrophy leads to profound changes at the morphological, physiological and genomic levels.

Results: Here, we characterize the transcriptomes of three species representing two lineages of mycoheterotrophic plants: orchids (*Epipogium aphyllum* and *Epipogium roseum*) and Ericaceae (*Hypopitys monotropa*). Comparative analysis is used to highlight the parallelism between distantly related fully heterotrophic plants.
In both lineages, we observed genome-wide elimination of nuclear genes that encode proteins related to photosynthesis, while systems associated with protein import to plastids as well as plastid transcription and translation remain active. Genes encoding components of plastid ribosomes that have been lost from the plastid genomes have not been transferred to the nuclear genomes; instead, some of the encoded proteins have been substituted by homologs. The nuclear genes of both *Epipogium* species accumulated nucleotide substitutions twice as rapidly as their photosynthetic relatives; in contrast, no increase in the substitution rate was observed in *H. monotropa*.

Conclusions: Full heterotrophy leads to profound changes in nuclear gene content. The observed increase in the rate of nucleotide substitutions is lineage specific, rather than a universal phenomenon among non-photosynthetic plants.

Keywords: Ericaceae, Loss of photosynthesis, Mycoheterotrophic plants, Nuclear genome, Orchidaceae, RNA-seq, Sequencing

Background

The capability for photosynthesis is the iconic trait of plants and is of the highest importance to the biosphere. However, some plants, including several thousands of flowering plant species, obtain organic substances from sources other than photosynthesis [1, 2]. These plants acquire organic compounds either from associated fungi (myco-heterotrophy) or by parasitizing other plants. Most of these species combine photosynthesis and heterotrophy, but several hundred species have totally lost photosynthetic ability and become fully heterotrophic. The acquisition of heterotrophic ability has occurred in the evolutionary history of plants more than 50 times [1, 2]. The switch to full heterotrophy leads to profound changes at the phenotypic level (reduction of leaves, loss of green colour, reduction of the vegetation period) that are highly parallel in different lineages. The genotypic alterations that underlie these changes are for the most part unclear. The difficulty of cultivating heterotrophic plants under experimental conditions hampers classic genetic and physiological studies. Advances in DNA sequencing permit the application of a genomic approach to elucidate the genetic changes associated with heterotrophy.

Genetic and genomic studies of heterotrophic plants are currently focused on two aspects. The first is the interaction of parasitic plants with their hosts and their adaptations to parasitism (e.g., [3]. Extensive exchange of transcripts occurs between hosts and parasites [4]. On an evolutionary scale, a large number of horizontal gene transfer (HGT) events from hosts to parasites have been found in the organellar and nuclear genomes of parasitic plants [5, 6]. A recent large-scale survey of HGT in

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